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Research Article

# Variation in root traits and phenotypic plasticity between native and introduced populations of the invasive plant *Chromolaena odorata*

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## Abstract

Understanding intraspecific trait variations, particularly for invasive species that occupy large geographic areas with different resource conditions, can enhance our understanding of plant responses to changes in environmental resources. However, most related studies have focused on aboveground traits, while variations in root traits and responses to changes in resources during biological invasion have not been clarified. To fill this knowledge gap, we compared the root traits of *Chromolaena odorata* from 10 introduced populations in Southeast Asia and 12 native populations in North and Central America under different soil nutrients. The introduced populations of the invader exhibited greater resource-acquisitive root traits, characterized by reduced fine root diameter but increased proportions of absorbing root length and specific root length, compared to the native populations. Although nutrient addition significantly affected root traits, the introduced populations showed greater phenotypic plasticity in four traits (root / shoot ratio, specific root length, absorbing root length proportion, and branching intensity) than the native populations. Different root trait syndromes were observed between the introduced and native populations. These results indicate that after introduction, *C. odorata* may shift towards a more soil resource-acquisitive strategy and thus respond more positively to increased soils nutrients, thereby showing better performance in high-resource environments. This study provides a better understanding of how species respond to environment changes and reveals the factors underlying exotic plant invasion success.

**Key words:** *Chromolaena odorata*, covariation, invasive species, phenotypic plasticity, root traits, soil nutrients

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## Introduction

Invasive species encounter diverse abiotic and biotic environmental conditions across their native and introduced ranges (Richardson and Pyšek 2006). The variation of traits within invasive species is constrained by both genetic differentiation and phenotypic plasticity, which reflects the evolutionary history and adaptation of these species to environmental conditions (Díaz and Cabido 2001). Understanding the extent of intraspecific trait variations along ecological gradients is essential for unraveling species' responses to environment conditions within the current

global change context (e.g., nitrogen deposition) (Weemstra et al. 2022; Gao et al. 2023). Various studies have explored intraspecific variations in aboveground functional traits (Feng et al. 2011; Zhao et al. 2020). However, few studies have investigated intraspecific variations in root traits despite their importance for the absorption of water and nutrients (Bardgett et al. 2014).

Fine roots (< 2 mm in diameter) represent the interface between plants and soil and thus have received increasing attention (Bergmann et al. 2020; Wang et al. 2021; Gao et al. 2023). Similar to the leaf economic spectrum, the suite of associated fine root traits may also reflect the resource acquisition strategy of a plant (Reich 2014; Weemstra et al. 2016). For example, root diameter, specific root length (root length per unit root dry mass), and specific root area (root area per unit root dry mass) are key traits for measuring plant resource investment in nutrient uptake (Makita et al. 2009). High specific root length, low root diameter, and low dry matter content are considered resource acquisitive traits that are generally associated with fast plant growth and reduced dependence on mycorrhizal fungi for nutrient uptake (Kong et al. 2014; Chen et al. 2016; Ma et al. 2018; Kong et al. 2019). In contrast, thick root diameter, low specific root length, and high root tissue density (root dry mass per unit root volume, reflecting root longevity) are considered resource-conservative root traits that are often associated with slow growth and increased dependence on mycorrhizal fungi for nutrient uptake (Eissenstat et al. 2015; McCormack and Iversen 2019; Bergmann et al. 2020). Soil environmental conditions (e.g., water content and soil nutrients) can affect root trait variation. For instance, in unfavorable environments (e.g., infertile and dry conditions), plants often show high root tissue density to increase root longevity (Ryser 1996; Eissenstat 2000). Intraspecific variations in root traits along an elevational gradient have been observed for 11 species; however, these patterns were species-specific (Weemstra et al. 2020).

Invasive species may encounter distinct selection pressures in their introduced habitats compared to those in their native ranges, potentially leading to variations in fitness-related traits (Keane and Crawley 2002; Joshi and Vrieling 2005; Schrieber et al. 2017). Some studies have found that invasive species shift toward a fast growth strategy (higher photosynthetic rate, specific leaf area, and leaf nitrogen) compared to their conspecifics from their native ranges (Mozdzer and Zieman 2010; Feng et al. 2011; Leishman et al. 2014; Heberling et al. 2016). Additionally, the introduction of invasive plants may also lead to changes in multiple co-varying traits known as "syndromes" (Kueffer et al. 2013; Tewes and Müller 2018; Liu et al. 2021). For example, Tewes and Müller (2018) discovered that *Bunias orientalis* from introduced populations with high silicle counts displayed increased leaf numbers and higher values in reproduction-related growth traits, whereas this syndrome was not particularly evident for conspecifics from native populations. In terms of belowground trait, Dawson (2015) hypothesized that a suite of root traits related to soil resource uptake ability may exhibit similar dynamics as leaf traits in invasive plants, potentially shifting toward roots with higher resource uptake strategy such as higher specific root length and lower diameter than those of their native conspecifics due to novel selection pressures encountered in introduced ranges. However, limited attention has been given to the variation and covariation of root traits among introduced and native populations of invasive species.

Phenotypic plasticity is often cited as a mechanism that facilitates invasion (Richardson and Pyšek 2006; Davidson et al. 2011). Alien plant species frequently

exhibit limited genetic variation due to their small population sizes upon introduction, and plasticity for important functional trait can facilitate the success of invasive plants across heterogeneous environmental gradients after introduction (Ghalambor et al. 2007; Liao et al. 2016). Bossdorf et al. (2008) found that invasive populations of *Senecio inaequidens* exhibited greater plasticity in root / shoot ratios compared to native populations when responding to nutrient addition, which may enhance their ability to efficiently utilize increased resource availability. Chun (2011) indicated that the invasive plant *Lythrum salicaria* showed significantly higher phenotypic plasticity for aboveground biomass in response to changing nutrient levels compared to the native conspecifics. Caño et al. (2008) also found that invasive plants *Senecio pterophorus* from introduced ranges demonstrated higher survival in disturbed environment than their conspecifics from native ranges, attributed to lower specific leaf area and better water content regulation of invasive populations under drought conditions. As a vital organ responsible for nutrient and water uptake from the soil, plastic responses of root traits can optimize nutrient acquisition and enhance plant performance (Larson and Funk 2016; Chen et al. 2023). However, most previous studies mainly focused on aboveground traits. Understanding the plasticity in root traits among invasive species populations could provide additional insights into how belowground resource strategies influence plant invasion under changing environmental conditions.

*Chromolaena odorata* (L.) R. M. King and H. Robinson (Asteraceae) is native to Central and South America, but it has become a noxious invasive shrub in Asia, Oceania, and Africa (Muniappan et al. 2005). It can invade different habitats across a wide environmental gradient (Kriticos et al. 2005). Studies have indicated that introduced *C. odorata* populations are better competitors than native populations (Zheng et al. 2015; Li et al. 2020), and exhibit faster growth economic traits such as higher photosynthetic capacity in introduced ranges compared to the native populations (Li et al. 2022). Molecular analysis revealed a low genetic variation among introduced populations of *C. odorata* (Yu et al. 2014), which is expected due to phenotypic plasticity facilitating their invasion across diverse environments. Liao et al. (2019) compared plasticity in aboveground traits of *C. odorata* among populations under different light treatments and found that the introduced populations had higher phenotypic plasticity for height, biomass, and total leaf area compared to their native counterparts but not for root / shoot ratio. Other studies showed that under high-nutrient conditions, invasive populations of *C. odorata* exhibited higher biomass (Li et al. 2020) or were more competitive (Qin et al. 2013) than their native populations, suggesting a more positive response by introduced populations to increased nutrient availability. These results provide insights into how aboveground traits vary among the invader populations and in their response to nutrient and light conditions. However, it remains unclear how root traits vary among introduced and native populations of the invader and how they respond to different nutrient conditions. Thus, we compared nine root traits of *C. odorata* from 10 introduced populations in Asia and 12 native populations in Central and South America under two nutrient levels. The following problems were addressed: (1) Do introduced populations shift towards more resource-acquisitive root traits (i.e., low diameter, high specific root length, and high branching intensity) when compared with the native populations? (2) How do root traits respond to soil nutrients? Do the introduced populations also exhibit greater phenotypic plasticity in response to high nutrient levels, similar to aboveground traits, compared to native populations?

## Methods

### Study site and materials

This study was conducted at the Xishuangbanna Tropical Botanical Garden (XTBG) (21°560'N, 101°150'E; 570 m elevation) of the Chinese Academy of Sciences, located in Mengla County, Yunnan Province, Southwest China. The Botanical Garden is located in the northern part of China's tropics. The mean annual temperature in this region is 21.7 °C, and the mean annual precipitation is 1557 mm, with a dry period from November to April (Feng et al. 2002).

In this study, 12 native and 10 introduced populations of the invader were compared (Table 1). Seeds of *C. odorata* were collected, germinated and grown in July 2010 at XTBG. For each population, the seeds were collected from 10–12 individuals from December 2019 to February 2020.

### Experiment design

*Chromolaena* can invade habitats with different nutrient conditions, such as low-nutrient roadsides with topsoil removed or high-resource wasteland due to disturbance or fertilization. We collected field soil from roadsides near the invader monoculture located in the XTBG and then simulated high-resource habitats by adding nutrients. The seeds were cleansed with 5% NaClO for surface sterilization for 10 min and sown in seedling trays with sand- and humus-rich soil (1:1) in March 2020 in a shade house

**Table 1.** Information about the sampled *Chromolaena odorata* populations.

| Code | Country/Region | GPS Coordinates | Elevation (m) |
|---|---|---|---|
| **Invasive populations** | | | |
| BK | Thailand | 14°25'N, 101°23'E | 739 |
| JD | Yunnan, China | 24°17'N, 100°50'E | 1263 |
| ML | Yunnan, China | 21°56'N, 101°15'E | 544 |
| MY | Melaka, Malaysia | 2°22'N, 102°21'E | 50 |
| PH | Iligan, Philippines | 8°10'N, 124°10'E | 107 |
| SL | Kegalle, Sri Lanka | 7°11'N, 80°25'E | 451 |
| SM | Yunnan, China | 22°46'N, 100°56'E | 1380 |
| SY | Hainan, China | 18°19'N, 109°12'E | 23 |
| WX | Vientiane, Laos | 17°58'N, 102°37'E | 170 |
| YNS | Southern Vietnam | 11°20'N, 107°24'E | 125 |
| **Native populations** | | | |
| MCD | Tamaulipas, Mexico | 23°40'N, 99°11'W | 600 |
| MCY | Chiapas, Mexico | 16°44'N, 93°09'W | 640 |
| CUB | Pinar del Rio, Cuba | 22°45'N, 82°50'W | 565 |
| FAK | Collier, Florida, USA | 25°52'N, 80°29'W | 1324 |
| FBRO | Broward, Florida, USA | 26°08'N, 80°06'W | 3 |
| FMAR | Martin, Florida, USA | 27°06'N, 80°15'W | 3 |
| FMD | Miami, Florida, USA | 25°38'N, 80°20'W | 3 |
| MIC | Michoacan, Mexico | 18°51'N, 103°37'W | 950 |
| PM | Manati, Puerto Rico | 18°12'N, 67°06'W | 103 |
| PP | Ponce, Puerto Rico | 18°12'N, 67°06'W | 103 |
| T1 | Mamoral, Trinidad | 10°27'N, 61°17'W | 63 |
| T2 | Felicity, Trinidad | 10°31'N, 61°25'W | 10 |

with 30% transmittance. Seedlings were transplanted into 2 L pots (one seedling per pot) when they were ~10 cm in height. The pots contained 40% sand and 60% field soil (total nitrogen (N): 2090 mg $Kg^{-1}$; available N: 7.79 mg $Kg^{-1}$; available phosphorus (P): 8.17 mg $Kg^{-1}$; available potassium (K): 281.48 mg $Kg^{-1}$). The seedlings were divided into two groups. One group was treated with compound fertilizer (Shanxi Shima Fertilizer Co., Ltd, Shanxi, China) at a rate of 100 mg available N + 100 mg available P + 100 mg available K $Kg^{-1}$ dry soil. The required amount of fertilizer was weighed, dissolved in 20 mL tap water, and poured carefully into each pot in April and May. The other group of the seedlings was treated with 20 mL tap water as the control. Five replicates were performed for each treatment. In total, we grew 220 seedlings [(10 invasive + 12 native populations) × 2 treatments per population × 5 seedlings per treatment].

The seedlings were randomly placed at an open site with full sunshine, irrigated daily after transplantation, and weeded when necessary. Two months later, all plants were harvested. The shoots of each plant were collected from the soil surface, dried in an oven at 60 °C for 48 h, and weighed. The roots of each plant were carefully washed using tap water in a 1 mm sieve and then further washed in a tray to remove the remaining soil particles.

## Root trait measurement

The fine roots (< 2 mm in diameter) of each individual were clipped, disentangled to prevent overlap, and hierarchically dissected into branch orders according to the protocol described by Pregitzer et al. (2002). Absorptive roots (first- and second-order roots) and other fine roots were scanned using a V700 scanner (EPSON Co., Ltd. Japan) at 1200 DPI as 16-bit grayscale images. The RhizoVision Explorer software was used to analyze root images (Seethepalli et al. 2021). The following morphological traits were assessed for absorptive and other fine roots: total length, surface area, diameter, branching intensity (number of branches per root length), and volume. The proportion of absorbing root length (ratio of absorbing root length to total fine root length) was also calculated. The fine root fresh weight was recorded; then, the fine roots were dried in an oven at 60 °C for 48 h and weighed to determine fine root dry matter content, specific root length, specific root area, and root tissue density. Thick roots were also dried in an oven at 60 °C for 48 h and weighed to determine the root / shoot ratio (ratio of total root dry mass to shoot dry mass).

## Statistical analyses

Principal component analysis (PCA) of the population mean trait values was performed to explore the associations among traits in the sampled populations. Mixed linear models were used to evaluate the effects of nutrients, ranges (introduced vs. native range), and their interactions on each variable, with nutrient treatments and ranges as fixed factors and populations nested within the range and q-scores as random factors. The population mean STRUCTURE q-scores were added as a random effect to account for the demographic history of the patterns of trait divergence in the mixed models (Li et al. 2022). The least significant difference (LSD) test was used to analyze the differences among groups. Furthermore, we calculated the root trait plasticity index using the following formula:

$$(T_a - T_c) / T_c) \times 100 \text{ (Fort et al. 2015)},$$

where $T_a$ and $T_c$ are the mean response values of each population after the nutrition addition and control treatments, respectively. One-way ANOVA was used to test the effect of range on plasticity index.

Pearson's correlation analysis was conducted for the data from each nutrient level and range to test the pairwise correlations among fine root traits. Before the analyses, we tested the normality and homogeneity of variance of each variable and transformed each variable if the assumption was not met. All analyses were performed using IBM SPSS Statistics for Windows 25.0 (IBM Corp. Armonk, New York, USA).

## Results

### Trait variation between ranges

PCA results showed distinct clustering patterns among populations of *C. odorata* according to their geographical origins and nutrient treatments, with significant overlap observed between the introduced and native populations across both nutrient levels along the first two principal components (Fig. 1). Notably, a substantial proportion of the variation was explained by the first and second axes (PC1 = 49.7%; PC2 = 21.5%). Furthermore, under different nutrient condition, populations exhibited separation primarily along the first principal component, which was mainly correlated with the specific root area, specific root length, root tissue density, fine root diameter, root / shoot ratio, and fine root dry matter content. Additionally, differentiation between populations from the introduced and native ranges was predominantly driven by variations in absorbing root length proportions, branching intensity, and fine root biomass along the second principal component.

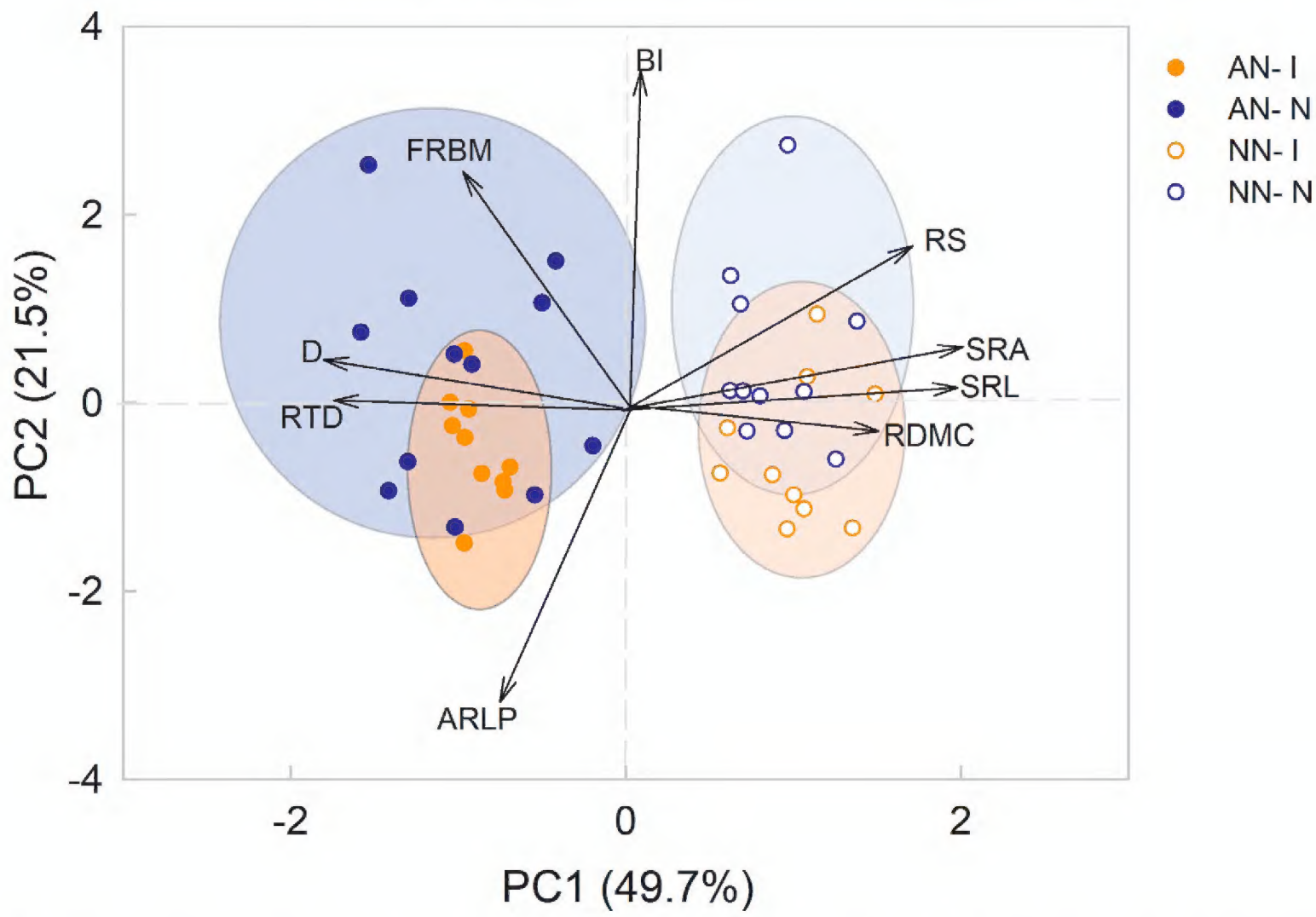


**Figure 1.** Biplot of principal component analysis (PCA) for the nine traits of 10 introduced (I, circles in orange) and 12 native (N, circles in blue) populations of *Chromolaena odorata* grown in soil with (AN, filled circles) and without (NN, open circles) nutrient addition. RS, root / shoot ratio; FRBM, fine root biomass; RDMC, fine root dry matter content; ARLP, absorbing root length proportions; SRL, specific root length; SRA, specific root area; RTD, root tissue density; BI, branching intensity; D, fine root diameter.

The range (introduced vs. native range) significantly influenced five out of the nine root traits (Table 2). The introduced populations showed higher root dry matter content but lower fine root diameters than the native populations under both soil nutrient levels (Fig. 2c, d). However, the biogeographical differences in the root / shoot ratio, absorbing root length proportions, and specific root length depended on soil nutrient levels (Table 2, Fig. 2a, d, e).

## Effect of soil nutrients on root traits

Soil nutrients significantly affected root traits (Table 2). Nutrient addition resulted in a decrease in the fine root dry matter content, specific root length, and specific root area, while it led to an increase in the root / shoot ratio, fine root biomass, root

**Table 2.** Effects of soil nutrients ($n$ = 2), ranges ($n$ = 2), and their interaction on nine root traits of *Chromolaena odorata*.

| Variable | Nutrient (N) | Range (R) | N × R |
|---|---|---|---|
| Root / shoot ratio | 192.79*** | 10.25** | 10.96** |
| Biomass of fine root (g) | 93.18*** | 3.96 | 1.24 |
| Root dry matter content (%) | 113.17*** | 7.16* | 1.88 |
| Branching intensity ($mm^{-1}$) | 3.14 | 0.50 | 11.51** |
| Absorbing root length proportion (%) | 14.78*** | 22.26*** | 7.70** |
| Specific root length ($m\ g^{-1}$) | 554.73*** | 8.24** | 6.74* |
| Specific root area ($mm^2\ mg^{-1}$) | 285.08*** | 0.50 | 2.515 |
| Root tissue density ($g\ cm^{-3}$) | 112.88*** | 0.04 | 0.41 |
| Diameter (mm) | 513.79*** | 24.22*** | 3.41 |

*, **, and *** refer to $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. Populations nested within ranges and q-values were used as random f actors.

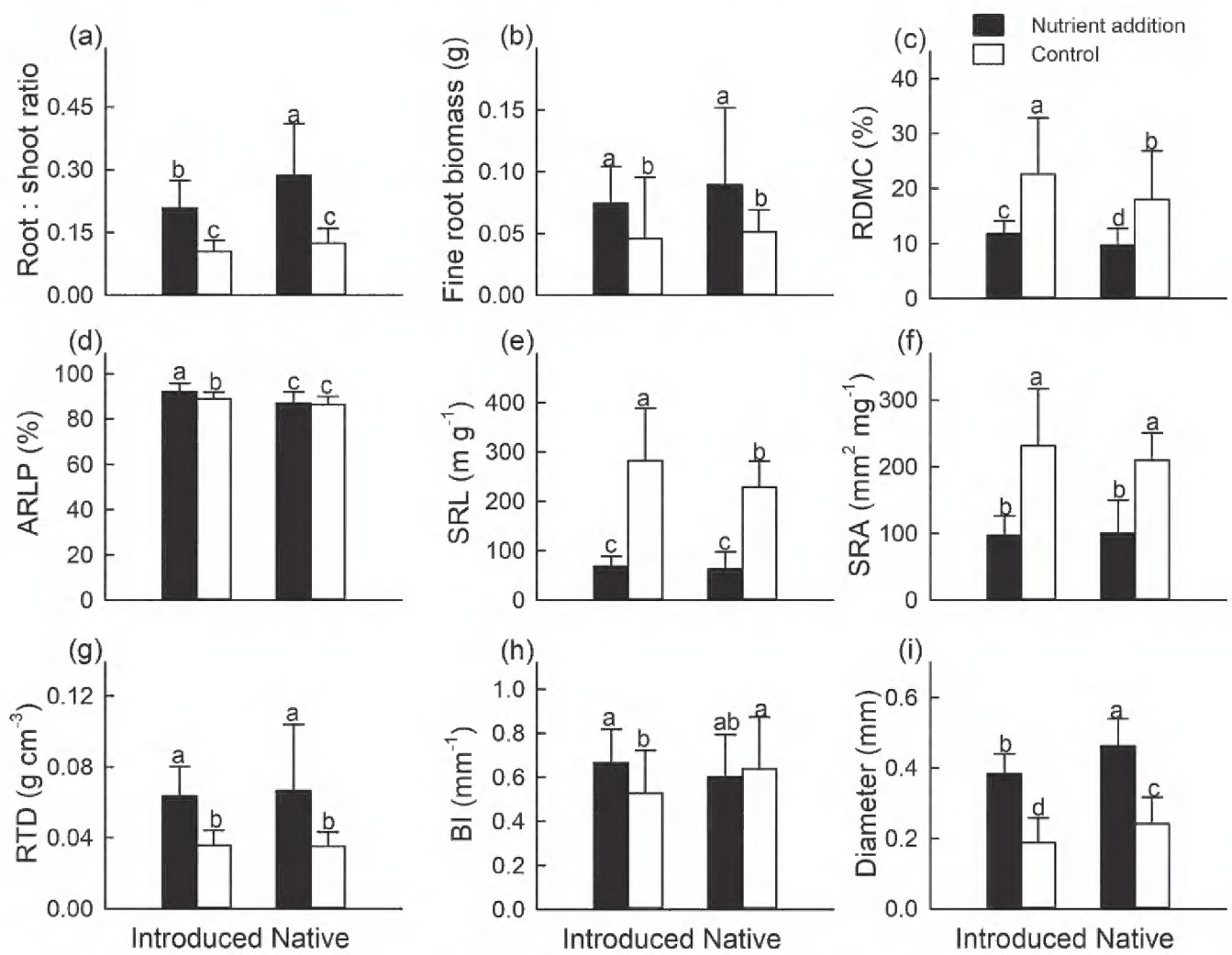


**Figure 2.** Root traits of *Chromolaena odorata* from the introduced and native populations in soil with (black bar) and without (white bar) nutrient addition **a** differences in the root / shoot ratio **b** fine root biomass **c** fine root dry matter content (RDMC) **d** absorbing root length proportions (ARLP) **e** specific root length (SRL) **f** specific root area (SRA) **g** root tissue density (RTD) **h** branching intensity (BI), and **i** fine root diameter.

tissue density, and fine root diameter of both introduced and native populations (Fig. 2). There were significant interactions between nutrient addition and range for plants from different ranges (as shown in Table 2), indicating distinct phenotypic plasticities between the introduced and native ranges (refer to Fig. 3). In soil with nutrient addition, the introduced populations exhibited higher proportions of absorbing root length and branching intensities compared to those without nutrient addition; however, no significant differences were observed for those traits among the native populations (Fig. 2d, h, Table 2). Furthermore, compared to the native populations, the introduced populations demonstrated higher plasticity in terms of root / shoot ratio and specific root length (Fig. 3a, e).

## Trait covariation

Trait covariation pattern differed among ranges and soil nutrient treatments. In the native populations, plants with increased root tissue density exhibited reduced specific root lengths and specific root areas in both soil nutrient level. Conversely, in the introduced populations, plants with increased fine root dry matter content showed reduced specific root areas only in soil without nutrient addition (Fig. 4). Within the introduced populations, increases in specific root length and specific root area were associated with enhanced branching intensity in soil without nutrient addition, while an increase in specific root length was linked to higher proportions of absorbing root length in soil with nutrient addition. A significant negative correlation between root diameter and absorbing root length proportion was observed for the introduced populations under both soil nutrient levels. More-

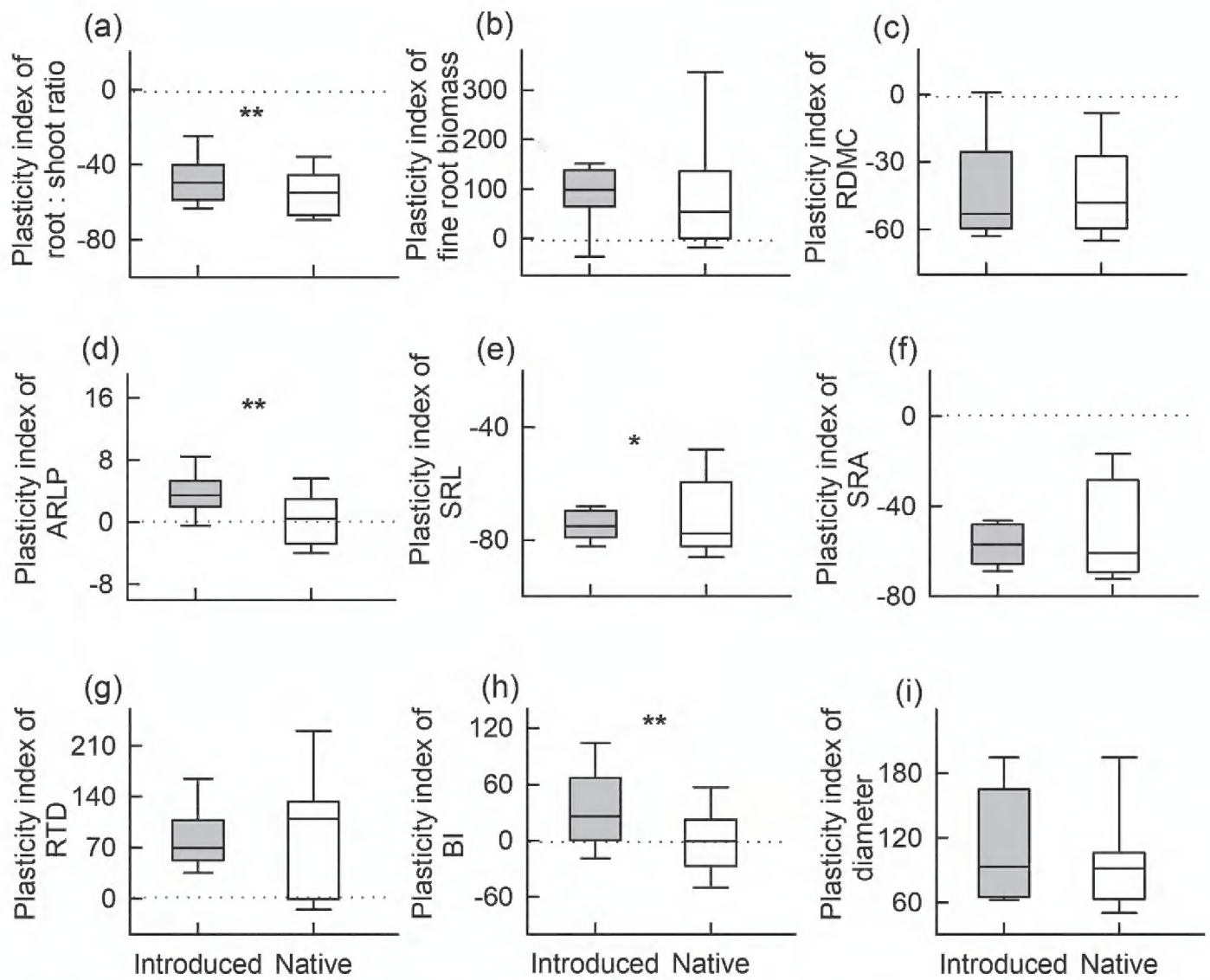


**Figure 3.** Plasticity index for root traits of *Chromolaena odorata* from the introduced (grey bar) and native (white bar) populations under two nutrient treatments **a** differences in the root / shoot ratio **b** fine root biomass **c** fine root dry matter content (RDMC) **d** absorbing root length proportions (ARLP) **e** specific root length (SRL) **f** specific root area (SRA) **g** root tissue density (RTD) **h** branching intensity (BI), and **i** fine root diameter.

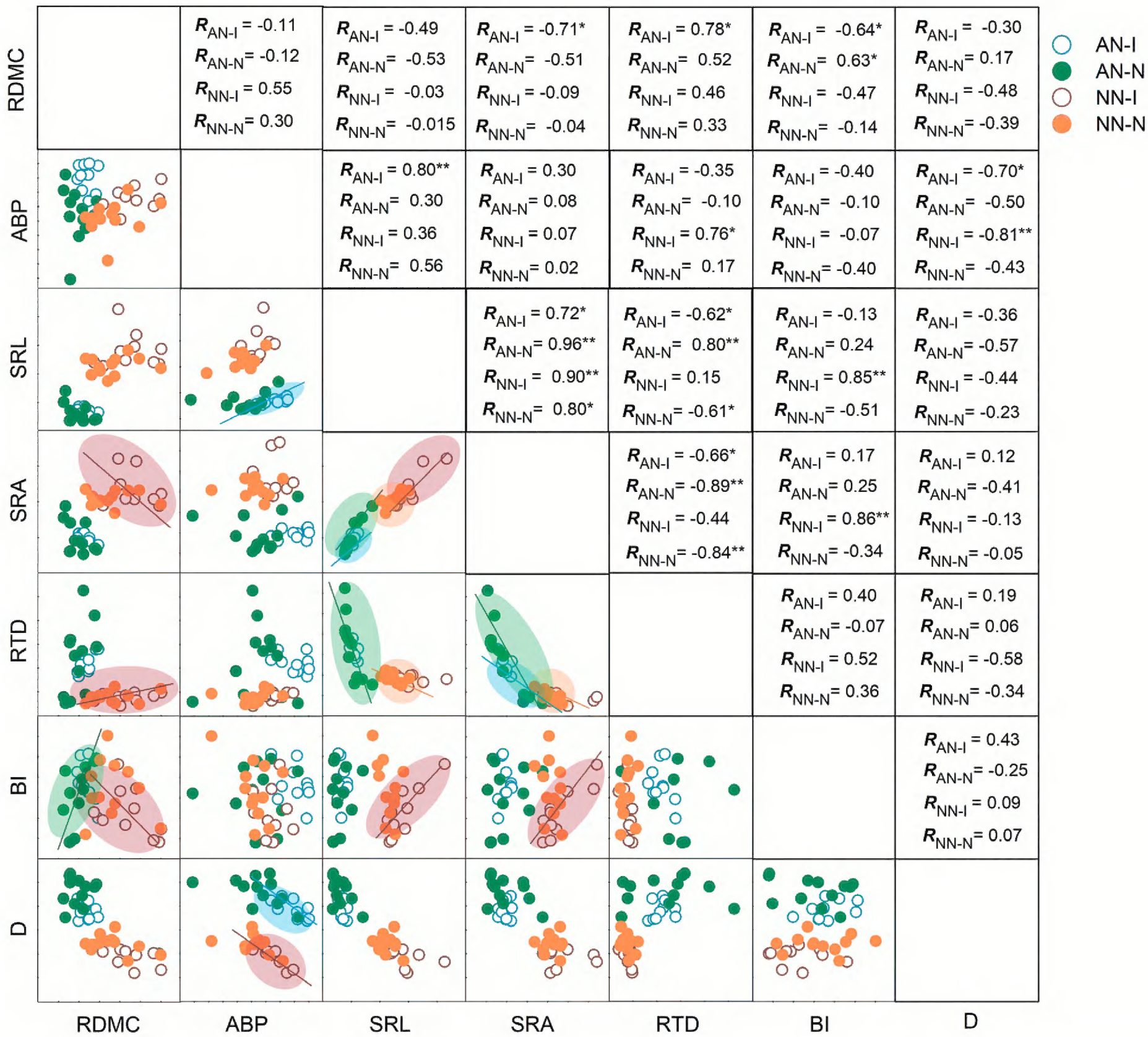


**Figure 4.** Pearson's correlation coefficient matrix for the seven root traits in the 10 introduced (I, open circles in blue and red) and 12 native (N, full circles in green and orange) populations of *Chromolaena odorata* grown in soil with (AN, circles in blue and green) and without (NN, circles in red and orange) nutrient addition. RDMC, fine root dry matter content; ARLP, absorbing root length proportions; SRL, specific root length; SRA, specific root area; RTD, root tissue density; BI, branching intensity; D, fine root diameter.

over, for the introduced populations, there was a negative correlation between root dry matter content and branching intensity in soil without nutrient addition but a positive correlation for the native populations in soil with nutrient addition.

## Discussion

To understand how root traits of invasive plants change in response to variable soil nutrient conditions during biological invasion, we compared the root traits of *C. odorata* from 10 introduced populations in Asia with those of 12 native populations from Central and South America under two nutrient levels. Our study provided the first evidence for divergence in root trait between introduced and native populations of an invasive species, while further elucidating the differential patterns of response exhibited by these root traits under varying nutrient levels between introduced and native populations.

## Variation in root traits between ranges

Our results provide support for Dawson's (2015) hypothesis that invasive species exhibit a shift in root traits towards resource-acquisitive roots, characterized by decreased root diameter and increased specific root length, in their introduced ranges owing to release from belowground specialist enemies. Specifically, the introduced populations of *C. odorata* displayed thinner roots and higher proportions of absorbing root length and specific root lengths (under low nutrient only) than the native populations across different soil nutrient levels. This indicates that a shift in root traits towards more resource-acquisitive roots may enhance soil resources' uptake and confer competitive advantage to the invaders over their new neighbors in introduced ranges. The study of Guan et al. (2023) on *Solidago canadensis* also demonstrated its ability to adjust nitrogen uptake strategy based on the contents and proportions of different forms of soil nitrogen, thereby promoting growth through enhanced nitrogen acquisition. Furthermore, many invasive plant species have been found to exhibit higher nitrogen and nutrient contents compared to their native counterparts (Huang et al. 2020; Liu et al. 2022).

A shift towards more resource-acquisitive roots may decrease enemy defense due to increased physical exposure to soil enemies and the trade-off between resource uptake and defense (Bauerle et al. 2007; Endara and Coley 2011; Rasmann et al. 2011). However, our results did not provide evidence for this prediction. Root toughness provides a direct physical barrier against herbivores (Johnson et al. 2010). The increased fine root dry matter content in the introduced populations may lead to an increase in resistance against soil enemies by enhancing root toughness. In this study, both nutrient conditions resulted in higher fine root dry matter content in introduced populations of *C. odorata* compared to native populations suggesting higher enemy resistance. One possible explanation is that invasive species may also exhibit defenses against generalist enemies in their introduced ranges, despite escaping from native specialists. Indeed, the rhizosphere soil of *C. odorata* from its introduced range in India showed an accumulation of local soil-borne pathogens, which are believed to have more negative effects on native species (Mangla and Callaway 2008). Consistent with these findings, Zheng et al. (2015) demonstrated that *C. odorata* plants from the introduced ranges show better resistance to natural enemies in the soil than those from the native ranges. These results indicate that the root strategy involving enhanced efficient resource uptake and stronger defense mechanisms contribute to the successful invasion of *C. odorata*.

## Response to soil nutrients

The introduced populations of *C. odorata* exhibited a greater diversity and higher plasticity in root traits in response to nutrient addition compared to the native populations. Following nutrient addition, the introduced populations exhibited an increase in both absorption root length proportion and branching intensities, leading to enhanced exploitation intensity under nutrient enrichment conditions. Conversely, these changes were not observed in the native populations. Moreover, the introduced populations also displayed greater plasticity for specific root length, indicating a more positive response to nutrient addition. These plastic responses may enhance the adaptability of the introduced population of *C. odorata* by maximizing their ability to exploit increased nutrient availability and thereby facilitating

aboveground growth. These findings provide an explanation for previous studies conducted by Qin et al. (2013) and Li et al. (2020), which reported that introduction populations of *C. odorata* demonstrated higher plastic in aboveground performance compared to native populations. The results are consistent with the hypothesis posited by Richards et al. (2006), proposing that successful establishment of invasive species can be attributed to their ability to enhance fitness through phenotypic plasticity in response to increased resource availability. The outcomes highlight the significance of phenotypic plasticity in root traits as a pivotal mechanism facilitating invasion of exotic species under changing environmental condition.

Our results also demonstrated that nutrient addition increased fine root biomass and induced changes in the morphological traits of fine roots. High specific root length, small diameter, and low root tissue density are often indicative of enhanced metabolic activity and an increased capacity for nutrient uptake (Eissenstat 2000; Roumet et al. 2016). However, our results revealed a significant decrease in specific root length and an increase in both diameter and root tissue density of fine roots under nutrient addition, suggesting a shift toward higher investment in structural support and reduced allocation to soil resource acquisition as a response to nutrient availability. This could be attributed to the fact that nutrient addition reduces the need for plants to allocate resources towards fine root for efficient nutrient absorption (Taylor et al. 2014). Conversely, the alterations observed in specific root length and root tissue density can be attributed to the increase in fine root biomass resulting from nutrient addition. The augmentation of fine root biomass has the potential to modify plant species' response regarding their ability to uptake additional available nutrients through modifications in their root surface area. This is supported by the functional balance hypothesis which suggests that plants must maintain a stable ratio between aboveground and belowground biomass resources for optimal overall plant performance (Thornley 1991). Du et al. (2020) demonstrated that nitrogen deposition promotes even further accumulation of root biomass within grassland ecosystems with nitrogen limitations. In conclusion, *C. odorata* responds to increased nutrient availability primarily through an augmentation of its fine root biomass rather than altering its fine root length.

### Changes in trait syndromes between ranges

Our study revealed significant correlations among the root traits; however, the patterns of trait covariation differed across ranges and soil nutrient levels. Principal Component Analysis (PCA) results indicated that the specific root area, specific root length, root tissue density, fine root dry matter content, and fine root diameter were subject to selection pressure by the nutrient conditions, while fine root dry matter content, branching intensity, and absorbing root length proportion were influenced by the different ranges. These findings suggest that distinct selection pressures can lead to diverse trait syndromes. Furthermore, novel environmental conditions in the introduced ranges may result in altered pattern of trait coordination (Messier et al. 2018). Trait syndrome reflects the adaptive strategies of plant species to different environmental conditions (Kueffer et al. 2013; Tewes and Müller 2018; Liu et al. 2021). In introduced population, plants with high specific root length and specific root area displayed increased branching intensity in soils without nutrient addition. This root syndrome indicates that plants from the introduced populations may enhance resource acquisition under low-resource conditions by increasing invest-

ments in the length of thinner roots and root networks. However, in native populations, plants with high root tissue density exhibited lower specific root lengths and specific root areas in soil with and without nutrition, suggesting a trade-off between resource-acquisitive and resource-conservative strategies for *C. odorata* within its native ranges characterized by high natural enemy pressure. Similar trade-offs were observed in the introduced populations grown in soil with nutrient addition. The distinct root trait syndromes between introduced and native populations imply the involvement of different adaptive strategies across different environments.

## Conclusion

The root traits of invasive populations of *C. odorata* exhibited enhanced capacity for soil resource uptake ability and superior adaptability to increasing soil resources compared to those of its native conspecifics. These findings suggest that belowground resource acquisition strategies play a pivotal role in the invasions' success of exotic plants, thereby enhancing our understanding of the mechanisms underlying invasive species.

## Additional information

### Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Yang-Ping Li: Designed and performed the experiments, analyzed the results, and wrote the paper. Wei-Tao Li: Analysis of the results and writing and review of the paper. Yan-Fen Niu: Performed the experiments. Yu-Long Feng: Writing and review of the paper.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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